"Livewood": Geomorphic and Ecological Functions of Living Trees in River Channels

JEFFREY J. OPPERMAN, MARK MELEASON, ROBERT A. FRANCIS, AND ROB DAVIES-COLLEY

Although the geomorphic and ecological importance of large wood in streams and rivers is well recognized, most studies consider only dead wood in channels. However, we have observed that living parts of trees are often found within active channels and that this "livewood" shares functions with both instream dead wood and live riparian trees, while also providing some functions unique to living woody material within a channel. We describe the mechanisms that produce livewood and illustrate its characteristics and influences on riparian and stream ecosystems with examples from Europe, North America, and New Zealand. We hypothesize that, compared with dead wood in channels, livewood (a) persists longer because of greater stability and greater resistance to decay, and (b) imparts greater structural complexity (with associated hydraulic roughness and retentiveness). The phenomenon of livewood implies that a broader range of tree species and sizes than previously considered may contribute functionally important wood to channels. We encourage the study of livewood in a range of forest-stream ecosystems to test our hypotheses and further our understanding of how forests interact with rivers and streams.

Keywords: large wood, stream ecology, channel morphology, riparian forest, forest-stream interactions

Wood—including trees, logs, rootwads, and branches—performs numerous geomorphic and ecological functions in streams and rivers throughout the world (Harmon et al. 1986, Gregory et al. 2003a). Recognizing the significant influence wood exerts on river ecology, the US National Research Council concluded, "Perhaps no other structural component of the environment is as important to salmon habitat as is large woody debris" (NRC 1996, p. 194).

Massive single logs or aggregations of wood, called jams, can strongly influence the morphology of channels—ranging from headwater streams to large rivers—by inducing step and pool formation, sediment deposition, channel avulsion, and island formation (Montgomery et al. 1995, 2003, Abbe and Montgomery 1996). Wood in stream channels—henceforth referred to as "streamwood"—serves important ecological functions, strongly linked to its geomorphic functions, such as trapping and retaining organic matter, thus providing habitat complexity and increasing the food supply for aquatic animals (Bilby and Likens 1980, Muotka and Laasonen 2002). Streamwood can be particularly important as habitat in sand-bed streams that lack gravel or other hard, stable substrates (Benke and Wallace 2003). Wood jams provide fish and crayfish with shelter from high flows and cover from predators (Murphy et al. 1986, Shirvell 1990, Giannico 2000).

Research on and management of streamwood has previously considered dead material almost exclusively (e.g., Krajick 2001). Field sampling protocols often limit data collection to dead wood (see examples cited in Opperman 2005), and typically assign wood pieces to a decay class that assumes the wood is dead (e.g., Robison and Beschta 1990). However, in a variety of forested streams worldwide, we have observed that streamwood can sometimes be living (figures 1, 2; Opperman 2005, Francis et al. 2006).

In this article we introduce the term "livewood" and define it, then illustrate its characteristics and influences on riparian and stream ecosystems through case studies from Europe, North America, and New Zealand. We demonstrate that livewood performs a range of functions in channels, sharing some of the functions of both dead wood in streams and live

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*Figure 1. (a) A living California bay (*Umbellularia californica*) spans the channel of Devil's Gulch (Marin County, California), leading to upstream sediment deposition and a downstream plunge pool in this important spawning stream for coho salmon (*Oncorhynchus kisutch*). (b) The tree is still rooted in the true left bank (right side of the photo); the livewood is highlighted in brown shading, including a vertically oriented branch that functions as a small riparian "tree," with foliage outlined by light green shading. Photograph: Jeffrey J. Opperman.*

riparian trees, while also providing some functions unique to living woody material within a channel (table 1). We then present testable hypotheses about the mechanisms by which livewood influences channels and ecosystem processes (box 1) and suggest where, on the basis of characteristics of aquatic systems, riparian forests, and climate, livewood may be a particularly important structural element. Finally, we propose a conceptual framework for the interaction between woody material and stream channels, one that encompasses live trees and dead trees in riparian zones, and streamwood, both dead and alive.

In this article we avoid the term "large woody debris," which is often applied to wood in streams, because "debris" implies "dead" and has somewhat negative connotations, whereas streamwood is of major importance to the ecological integrity of forested streams. Following other researchers, we adopt the simpler terms "wood" (e.g., see the preface of Gregory et al. 2003a) or "streamwood."

Livewood definition

Conceptually, we define livewood as living woody material within a channel that is at least partially submerged at bankfull flow (the flow at which the stream just begins to flood over the lower of its two banks). An operational definition of livewood, for sampling and monitoring, will generally require setting a minimum size, as is commonly done for dead wood. For example, in the US Pacific Northwest, the operational term "large wood" is commonly defined as wood with a length greater than 1 meter (m) and small-end diameter greater than 10 centimeters (Harmon et al. 1986), and livewood could be similarly defined. We acknowledge that although such criteria are somewhat arbitrary, they are necessary to establish an operational sampling protocol. The relationship between wood dimensions—dead or alive—and functionality is not discrete but a continuum based on channel dimensions, stream power, the position of the wood, and other factors. This is important because, as discussed below, the characteristics of livewood that increase its stability may also allow it to be geomorphically functional at smaller dimensions than dead wood. For elements of wood that extend above the bankfull level, such as living trees growing out of a wood jam, we recommend recording in separate categories the dimensions of wood within the channel versus that outside the channel (e.g., Opperman 2005). This will facilitate inclusion of livewood in standard wood survey protocols and allow for more meaningful comparisons with previous work.

Livewood is derived from riparian trees through multiple mechanisms; for example, trees can grow into the active channel or enter it through bank erosion or other geomorphic processes (figure 3; the active channel is defined as the area that is normally inundated by seasonal high flows and corresponds to the "zone of scour" described by Poole et al. 2002). In some cases, trees fall into the channel, frequently because of bank erosion, but remain rooted and living. These trees can often reorient major branches as stems growing toward sunlight (figure 1). Livewood can also derive from trees that were uprooted and transported by flows, deposited at a new site, and then resprouted roots and stems (figure 2). Trees or other woody plants, such as lianas, that grow into the channel (figure 4) can also function as livewood. Although we do not address them in this article, several other sources of live woody material can interact with streams, including pneumatophores (or "knees") of bald cypress trees (*Taxodium distichum*), mangrove root systems, and tree roots that have been exposed through bank erosion (figure 3).

Table 1. Geomorphic and ecological functions provided by trees, livewood, and instream dead wood.

Function	Living riparian trees	Dead riparian trees	Instream livewood	Instream dead wood
	Woody components involved in forest-stream interactions			
Hydraulic roughness	During high flows that inundate riparian vegetation	During high flows that inundate riparian vegetation	During a range of flows	During a range of flows
Channel morphology	Bank stabilization by tree roots		Sediment deposition and storage	Sediment deposition and storage
	Pool formation (rootwads on bank can form lateral scour pools)		Pool formation	Pool formation
			Bed heterogeneity (e.g., step in long profile)	Bed heterogeneity (e.g., step in long profile)
Riparian forest regeneration	Vegetative and sexual reproduction		Vegetative and sexual reproduction	Island formation leading to forest succession
			Island formation leading to forest succession	
Structure	Vertical structure within riparian corridor	Vertical structure within riparian corridor	Horizontal and vertical structure in both riparian corridor and channel	Primarily horizontal structure in channel
Habitat	Substrate for invertebrates (primarily terrestrial)	Substrate for invertebrates (primarily terrestrial)	Substrate for invertebrates (aquatic and terrestrial)	Substrate for invertebrates (aquatic and terrestrial)
Shading	Shading of channel		Shading of channel (can provide similar shading as standing riparian trees if livewood includes vertical branches with leafy canopy)	Very local shading
Allocthonous inputs (e.g., leaves, twigs, branches)	Allochthonous inputs		Allochthonous inputs	

Case studies

A common framework for understanding wood dynamics uses a ratio of wood size to channel width to classify streams as small, medium, or large, and posits that the mobility, distribution, and geomorphic and ecological influences of wood vary among these stream sizes (Gurnell et al. 2002). For example, in small streams, most wood pieces are stable and remain where they enter the stream, whereas in large streams, nearly all wood is mobile and tends to be distributed along channel margins. Within medium-sized streams, wood tends to aggregate in wood jams behind large, stable key pieces (Keller and Swanson 1979, Gurnell et al. 2002). We present case studies of livewood from streams that range in size from small (New Zealand) to large (a braided river, the Tagliamento in Italy), and then suggest a series of hypotheses about livewood functions, including how it differs from dead wood in terms of its mobility, persistence, and scaling relationships with channel size.

Box 1. Hypotheses concerning livewood's characteristics and influence on channels and aquatic and riparian ecosystems.

Compared with dead instream wood of similar dimensions, livewood will have the following:

- Greater persistence in channels because of its greater decay resistance.
- Greater persistence in channels because of its greater stability.
- Greater structural complexity, hydraulic roughness, and retentive capacity.

Considerations regarding livewood's influence on channels and ecosystems:

- Livewood can be important only where riparian corridors contain trees with the ability to continue living and growing after entering the channel.
- Livewood will be particularly important in systems in which the riparian tree species produce dead wood with low persistence.
- Livewood, in the form of fluvially deposited trees that resprout, will be relatively important in systems in which riparian tree generation from seed is constrained.
- Livewood is expected to be relatively *unimportant* where the wood supply to streams is dominated by dead wood produced by very large trees.

Livewood will alter the scaling relationships between wood dimensions and channel size.

Figure 2. An example of livewood along the Tagliamento River in Italy. This Populus nigra *tree has been deposited on a gravel bar in one of the middle active channels of the river, where it has resprouted along the trunk and begun to modify its environment by trapping fine sediment. Photograph: Robert A. Francis.*
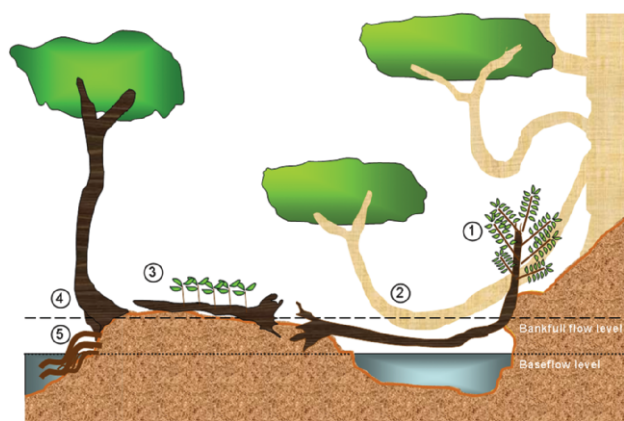

Figure 3. A schematic stream cross section, illustrating different mechanisms that produce livewood. (1) A tree that has entered the channel because of bank erosion, but remains living and produces new canopy foliage from vertically growing branches or sprouts; (2) a tree rooted on the hillside that has "draped" into the active channel, as kamahi and rata do in New Zealand or California Bay in northern California; (3) a tree (e.g., Populus *sp.) that has been fluvially deposited on an island at the edge of the active channel and begins to sprout; (4) a tree that has established at the edge of the active channel, providing woody instream structure during high flows; and (5) tree roots exposed by bank erosion.*

Livewood in small streams of Stewart Island, New Zealand.
Livewood and dead wood were surveyed in four streams in Abraham's Bay, Stewart Island (south of South Island, New Zealand, 46 degrees latitude South), although only the results from the dead-wood surveys have been published previously (Meleason et al. 2005). The surveyed streams ranged in mean bankfull widths from 2.6 to 5.8 m and had basin areas that ranged from 110 to 580 hectares. We report here the results for livewood and constrast them with the results from the dead-wood surveys.

New Zealand's forest composition has very little in common with temperate regions of the Northern Hemisphere (Takhtajan 1986), and, in particular, forests lack riparian specialist genera such as *Salix* and *Populus.* New Zealand's riparian forests, in common with lowland forests generally, consist of an emergent layer dominated by conifers from the Podocarpaceae family (e.g., *Dacrydium cupressinum*) and a canopy layer composed of hardwoods, among which tropical or subtropical tree genera are well represented (e.g., *Macropiper, Metrosideros, Elaeocarpus, Dysoxylum,* and *Alectryon*) (Takhtajan 1986). Vegetation forms characteristic of the tropics, such as tree ferns, palms, and lianas, are common.

Six out of 17 tree species in Stewart Island riparian zones were found as livewood within the active channels (e.g., living prostrate trees interacting with the stream at or below bankfull flow). Livewood included representatives of all canopy strata, such as *D. cupressinum* in the emergent layer,

Figure 4. Livewood in "Stream One," Abraham's Bay, Stewart Island, New Zealand. The prostrate live bole (a) of a **Metrosideros umbellata** *was rooted in, and thus stabilized, the near bank (out of picture); the part of the tree spanning the channel interacted with high flows. Numerous branches along the main trunk grew to canopy height, providing shade, litter, and terrestrial habitat. Several* **M. umbellata** *branches (b) growing out of a main bole (out of picture) are partially submerged at baseflow and also reach canopy height. Photograph: Rob Davies-Colley.*

Weinmannia racemosa in the dominant canopy, and tree ferns in the subcanopy layer. The two most common livewood species were rata (*Metrosideros umbellata*) and kamahi (*W. racemosa*), which often grow sideways or even downward as they extend toward the canopy gap above channels. As a result, trunks frequently encroach or "drape" into the active channel (figure 4).

Tree ferns, which can reach 20 m in height, are often significant components of New Zealand forests (Large and Braggins 2004) and contribute to both live and dead streamwood (Meleason et al. 2005). The tree-fern "stems" (fibrous root bundles) can armor a stream bank when growing in the channel or on the bank. The growth response after tree ferns have fallen into channels suggests that they survive for extended periods and persist within the channel.

Dead wood frequency ranged from 28 to 66 logs per 100 m, and the in-channel volume of dead wood ranged from 92 to 157 m³ per hectare (ha) (Meleason et al. 2005). Livewood averaged 26 percent (range: 13 to 34 percent) of in-channel wood volume and 9 percent (range: 3 to 14 percent) of wood frequency. More than one third of livewood elements (35 percent) had a direct geomorphic interaction with the streambed (e.g., causing erosion or sediment deposition) or bank (bank armoring or deflecting flow to erode the bank; see Meleason et al. 2005 for geomorphic categories).

The dead wood ranged in length from 1 to 16 m, and 47 percent of the pieces (80 percent of the volume) were classified as stationary (Meleason et al. 2005). Livewood ranged in length from 1 to 12 m, and there was no evidence that any of the livewood had moved downstream. This suggests that even within these small streams, where only the smallest pieces of wood are mobile, livewood was more stable than dead wood across a range of piece sizes.

Livewood as key pieces in medium-sized streams in Northern California. Large instream wood performs numerous functions important to anadromous salmonids during the freshwater portion of their life history (NRC 1996), and these benefits to salmon provided much of the original motivation for research on streamwood. Many studies have been done in the US Pacific Northwest, where streamwood is dominated by dead wood from very large conifers (Bilby and Ward 1991). In these systems, researchers considered riparian angiosperms too small or too quickly decaying to contribute significantly to the supply of functional streamwood (Swanson and Lienkamper 1978, Roni et al. 2002), although other research suggests that angiosperms can provide functional instream wood in small streams (e.g., streams with drainage area less than 800 ha; Keim et al. 2002).

In coastal watersheds of northern California, anadromous salmonids use streams within both conifer forests and, further inland, angiosperm-dominated forests. Opperman (2005) investigated the relationship between wood and salmonid habitat in these angiosperm-dominated forests, where the primary riparian tree species include California bay laurel (*Umbellularia californica*), white alder (*Alnus rhombifolia*), big-leaf maple (*Acer macrophyllum*), canyon live oak (*Quercus chrysolepis*), and willows (*Salix* spp.).

In these streams (bankfull widths ranging from 3.3 to 9.3 m; drainage area ranging from 340 to 4200 ha), a high proportion of the wood performing geomorphic functions is living (figure 1; Opperman 2005). Several lines of evidence suggest that livewood has greater stability and persistence than dead wood in channels. First, although livewood represented only a small percentage of wood frequency (10 percent of all wood elements), channel-spanning jams were more likely to have a living key piece (44 percent of channel-spanning jams had a living key piece) than a dead key piece (30 percent; the percentages do not sum to 100 percent because a key piece was not always identifiable). Furthermore, livewood can function as a key piece at smaller dimensions than can dead wood (Opperman and Merenlender 2007). Channel-spanning jams are subjected to the full energy of high flows, and the high prevalence of living key pieces suggests that livewood's stability—due to an attached, living rootmass—is an important factor in jam creation and stabilization. In these streams, channel-spanning jams provide much of the geomorphic and ecological function (e.g., storing wood and organic matter, creating pools, and providing cover), and thus livewood is a key influence on channel geomorphology and ecological processes (Opperman 2005).

In addition, repeat surveys on four of the streams, only one or two years after the initial survey, found that jams with livewood elements are much more persistent than jams containing just dead wood. Although the intervening winters had only moderate flood flows, 26 percent of the dead-wood jams had been washed out (48 out of 65 persisted) while only a single jam that contained livewood had disappeared (43 out of 44 persisted; Opperman and Merenlender 2007). This suggests that jams containing livewood may be generally more persistent than jams containing only dead wood.

In coastal northern California, riparian angiosperms provide dead wood that is smaller (Opperman 2005) and decays faster than dead conifer wood (Cederholm et al. 1997). However, livewood from riparian angiosperms can provide functional streamwood that exerts a significant influence on channel form and aquatic habitat (Opperman 2005, Opperman and Merenlender 2007).

Livewood and island development in a large river system: The Tagliamento River.
The Tagliamento River in northeastern Italy retains a natural morphology and a high degree of connectivity with its floodplain; it is characterized by abundant living and dead large wood deposited on exposed bars along its length (e.g., Tockner et al. 2003, Gurnell et al. 2005).

Several reaches of the river are heavily island-braided, in particular, the widely-researched 6.5-kilometer (km) pre-Alpine reach between Cornino and Pinzano bridges, where the active zone of the river is more than 1.2 km wide and low flow channels are 20 to 30 m wide (e.g., Tockner et al. 2003). Abundant evidence exists to link the inception, development, and maintenance of these river island landforms to the deposition of living wood (Edwards et al. 1999, Gurnell et al. 2001, 2005).

Common riparian tree genera along the river, such as *Populus, Salix,* and *Alnus,* are well documented for their ability to regenerate vegetatively from wood fragments and whole fallen trees (Gurnell et al. 2005, Francis et al. 2006). During floods, mature riparian trees are commonly removed, transported, and deposited on exposed bars downstream as flows recede (e.g., Edwards et al. 1999).

These trees create geomorphic features and habitat microsites that may be particularly important for ecological communities along the river; for example, scour features often form pools, which provide refuges for fish and invertebrates (e.g., Tockner et al. 2003). The deposited trees induce fine sediment deposition and trap plant seeds and fragments, promoting plant establishment and growth (Francis et al. 2008). The deposition of fine sediment greatly improves conditions for tree establishment relative to the predominant bar substrate of coarse gravel and cobble, which have low moisture retention (e.g., Dixon et al. 2002, Francis and Gurnell 2006).

However, the capacity for the fluvially deposited trees to influence their immediate physical environment is greatly increased if the trees are living when they are deposited. Under suitable conditions, with access to moisture and nutrients, and with minimal short-term disturbance, living deposited trees may survive, sprout, and establish on the bars (figure 2; Francis 2007). Growth rates and biomass production can be substantial (Francis et al. 2006), and the process of establishment has three key effects: (1) the production of deep and extensive rooting systems, characteristic of these species, leads to greater stability—relative to dead wood—of the deposited livewood and its associated geomorphic features (e.g., scour and bar aggradation); (2) the production of many tall shoots and dense foliage along the deposited trunk greatly increases the trapping of fine sediment and fine organic matter in subsequent high-flow events, increasing the rate of bar aggradation; and (3) the continued deposition of fine sediment buries the original tree in a medium more conducive to water retention and root growth, which further helps to anchor the tree. Simultaneously, the stems sprouting from the trunk produce adventitious roots in the aggrading sediment that surrounds them, and so continued shoot growth is encouraged (Gurnell et al. 2005).

Over time, this complex of deposited livewood, sprouting regeneration, and accumulated sediment and organic material tends to develop into small islands (Tockner et al. 2003, Gurnell et al. 2005), which may build and expand to amalgamate with other islands and form large "established" islands. These features have a dramatic and lasting influence on the

morphology and ecology of the river (Gurnell and Petts 2002, Tockner et al. 2003, Gurnell et al. 2005).

Regeneration from deposited trees is a primary mechanism encouraging island formation, and thus livewood is particularly important to the geomorphology of this system. The mechanisms for pool and island formation in the Tagliamento are similar to those described for the braided Queets River, Washington, by Abbe and Montgomery (1996), who noted that the process of large wood influencing island development required "the recruitment of key members from among the largest trees in channel-margin forests." Thus, in the Tagliamento, the greater stability afforded by livewood allows smaller wood elements to play geomorphic roles similar to that of much larger dead wood in the Pacific Northwest. Research is needed to quantify the role of living wood in island development, and determine factors that promote this kind of livewood function.

Hypotheses regarding livewood

These case studies, encompassing a range of stream sizes and riparian forest types, illustrate several common traits of livewood. In box 1 and in the text below we propose a set of hypotheses concerning livewood's characteristics and its influence on channels and aquatic and riparian ecosystems. We have preliminary data supporting some of these hypotheses, but we encourage testing in a broad range of systems.

The first category of hypotheses: Mechanisms by which livewood contrasts with dead wood in its influences on fluvial geomorphic processes and aquatic ecosystems. Compared with dead instream wood of similar dimensions, we hypothesize that livewood will have the following:

- **Greater persistence in channels as a result of greater decay resistance.** Living wood has greater decay resistance than does dead wood, and thus instream livewood should have greater decay resistance than instream dead wood. Microbial decay affects the mechanical strength of dead wood, increasing its susceptibility to fragmentation and abrasion by sediment during floods (Harmon et al. 1986). In contrast, livewood could potentially *increase* in strength through time as its size and root anchoring increase. We do not have data that directly support this hypothesis, but it should be relatively easy to confirm through experiments or field observations. As a result of increased resistance to decay and greater structural strength, and consequently lower rates of breakage and transport, livewood should persist longer in channels than dead wood does.

- **Greater persistence in channels because of greater stability.** The living, attached root system serves to anchor livewood in the channel bed or banks, providing greater ability to resist displacement and transport during high flows. Livewood's enhanced stability is indicated by the high proportion of living key pieces among channel-spanning jams in northern California, and by the greater persistence of wood jams containing livewood in comparison with those without living wood elements (described earlier and in Opperman and Merenlender 2007). Although resistance to decay most likely also contributes to persistence, in this study, jam persistence was evaluated after an interval of only 1 to 2 years (too short for appreciable decay), suggesting that stability rather than decay resistance contributed to greater persistence during the study period.

- **Greater structural complexity, hydraulic roughness, and retentive capacity.** Because of sprouting and regrowth, livewood frequently includes elements with both horizontal and vertical components (figures 1–4). While dead wood can have structural complexity through major branches from a bole, the major branches of livewood should be more persistent than those on dead wood, for the reasons discussed above. Opperman and Merenlender (2007) found that living wood elements were significantly more likely to have major branching than were dead wood elements. Such branching is expected to promote retention of large and small wood, plant propagules, other organic material, and sediment. In turn, this increased retentiveness may have implications for aquatic food webs, nutrient cycling, instream habitat, island formation, sediment transport, riparian regeneration, and plant community structure.

The second category of hypotheses: Where livewood will be particularly important. Collectively, the basic characteristics of livewood noted above suggest a further category of hypotheses regarding the types of ecosystems where livewood may be particularly important to channel morphology and ecological processes.

Livewood can be important only where riparian corridors contain trees with the ability to continue living and growing after entering the channel. From our observation, these trees include many common riparian genera (e.g., *Salix* and *Populus*), which is not surprising because riparian species generally show adaptations to high-disturbance environments, notably vegetative reproduction (Barsoum 2001, Karrenberg et al. 2002, Francis 2007). Several other riparian species have been observed exhibiting this flexible growth form, including big-leaf maple, Oregon ash, and California bay in California, and kamahi, rata, and tree ferns in New Zealand. Woody plants that extend major branches into the active channel, among them lianas and some tree species such as California bay and kamahi, can also produce livewood (figures 3 and 4).

Livewood will be relatively important in systems in which riparian tree species produce dead wood that tends to have low persistence. The low persistence of dead wood can be due to high transport rates (a function of wood dimensions and stream power) or rapid decay (due to characteristics of the wood or climate), or to both. In such systems, dead wood will

tend to be unstable or ephemeral and thus have less influence on channels and aquatic ecosystems. Therefore, in these systems livewood has more potential than dead wood to provide a greater range of functions.

Livewood, in the form of fluvially deposited trees that resprout, will be relatively important in systems in which riparian tree regeneration from seed is constrained. Regeneration of riparian trees by seed can be constrained by harsh riparian environments (e.g., aggrading gravel bars), unsuitable hydrological dynamics (e.g., in years when seed dissemination and establishment are restricted by a lack of high flows during periods of seed production and viability), or by frequent scour and erosion, which removes shallow-rooted seedlings (Barsoum 2001, Karrenberg et al. 2002, Rood et al. 2003, Douhovnikoff et al. 2005, Francis 2007). In such systems, vegetative reproduction from livewood can be more successful than recruitment from seed because sprouts from livewood have higher growth rates than seedlings do (Sigafoos 1964, Karrenberg et al. 2002, Francis 2007). Further, because livewood is continually viable, tree recruits from livewood can potentially regenerate over a greater spatial and temporal range than can those from seeds (Barsoum 2001).

Livewood's influence on local geomorphic patterns and processes such as sediment erosion and aggradation also influence the distribution and dynamics of riparian plant communities (Gurnell et al. 2005, Francis et al. 2008). Livewood is also likely to be more important than vegetative regeneration from small branches or other fragments, which are further mechanisms through which trees capable of vegetative reproduction cope with fluvial disturbance and a lack of sexual regeneration (Rood et al. 2003). Compared with branches, whole deposited trees have greater growth rates and stability and more effectively trap fine sediment and organic matter, and thus are most likely a far more effective regeneration mechanism (Francis et al. 2006).

Livewood is expected to be relatively *unimportant* where the wood supply to streams is dominated by dead wood produced by very large trees. For example, in streams within conifer forests of the US Pacific Northwest, very large redwood (*Sequoia sempervirens*) and Douglas fir (*Pseudotsuga menziesii*) trees dominate wood dynamics, most likely masking the contribution of trees capable of livewood function (e.g., alders and willows).

The final hypothesis concerns the implications of livewood for a primary conceptual model for streamwood.
This conceptual model seeks to explain how wood distribution, dynamics, and functions vary with channel size (Keller and Swanson 1979, Gurnell et al. 2002).

Livewood will shift the scaling relationships between wood dimensions and channel size. Wood stability (i.e., ability to resist fluvial transport) is central to streamwood conceptual models, which posit that wood dynamics, distribution, and functions are strongly influenced by the disturbance regime (Nakamura et al. 2000) and the relative mobility of wood pieces within a channel network (Keller and Swanson 1979).

Because the movement of (dead) wood is largely a function of the ratio of piece length to channel width (Nakamura and Swanson 1994), channels can be scaled on the basis of the distribution of piece sizes of their wood supply (Gurnell et al. 2002): within small channels, most wood will be stable (median piece length exceeds channel width); within medium channels, most wood is mobile but, because some pieces can span the channel, wood will accumulate in jams behind these key pieces (upper quartile of wood length distribution exceeds channel width); within large channels, all wood is mobile and tends to aggregate along channel margins (channel width exceeds maximum piece length).

Besides length, factors such as partial burial (Young 1994) or the presence of a rootwad (Braudrick and Grant 2000) can increase the stability of wood pieces. We hypothesize that livewood will alter the scaling relationships described above because the attached, living root system very strongly influences piece stability. This greater stability will be most apparent in medium and large rivers, because only very small wood is mobile in small channels. We hypothesize that livewood will increase the width of channel characterized by medium-channel wood dynamics (i.e., most wood volume found in jams behind key pieces) beyond what would be expected based on the distribution of dead wood supplied by the riparian corridor. The smaller size and stability of live key pieces compared with dead key pieces, as found in northern California, provide initial support for this hypothesis (Opperman and Merenlender 2007).

In large rivers, wood tends to aggregate near roughness elements such as bars and vegetated islands. Individual pieces of wood can serve as a roughness element and influence channel morphology if they can resist transport during high flows. For example, very large dead trees, with their rootwads oriented upstream, can induce upstream pool formation and downstream deposition and island creation in braided rivers (Abbe and Montgomery 1996). As described above in the Tagliamento case study, the stability provided by vigorous root growth can allow fluvially deposited livewood to perform similar functions with much smaller relative dimensions of piece size to channel width (Gurnell and Petts 2006). Finally, although most wood—living or dead—will be stable in small channels, the enhanced decay resistance of livewood will influence wood loading and dynamics in small channels.

Forests and channels:
From living trees to dead wood
We propose that interactions between wood and channels involve four components: (1) living standing trees, (2) dead standing trees, (3) livewood, and (4) dead wood in channels. These various woody components have a broad range of functions in riverine ecosystems, many of which overlap (table 1). For example, livewood shares several channel morphology functions with dead wood, but also shares functions with living riparian trees, such as allocthonous inputs and channel shading. These four woody components are distributed along a lateral gradient ranging from distal

portions of the floodplain, where wood interacts with flows only infrequently, to below the baseflow stage in channels, where wood contacts water in nearly all flow conditions. Through channel migration or avulsion, woody components distributed throughout the floodplain can interact over time with the active channel.

The four components of wood in table 1 interact strongly with each other, and the elements of one component influence the distribution and dynamics of the other components. For example, living riparian trees are the source of the other three components, and instream livewood will eventually become dead wood. Further, living trees along channel margins and key pieces (live and dead) can trap dead wood in fluvial transport, leading to wood accumulations and increasing the residence time of instream wood (Opperman and Merenlender 2004). Livewood can serve as a source for vegetative regeneration of the riparian forest, and large wood jams also can promote forest regeneration (Abbe and Montgomery 1996).

There is an extensive literature on the interaction between river channels and riparian vegetation (Gregory et al. 1991, Hupp and Osterkamp 1996) and on the interaction between instream wood and river channels (Gregory et al. 2003a and references therein). The framework described here—which views riparian trees, livewood, and dead wood as distinct but intergrading components—highlights the diverse ways in which woody material, channels, and aquatic and riparian ecosystems interact with and influence each other.

We postulate that livewood serves important geomorphic and ecological roles in forested streams and rivers. The distinctive characteristics of livewood, particularly its enhanced stability and persistence, may increase the relative importance of streamwood where riparian trees provide mostly small or rapidly decaying dead wood. The phenomenon of livewood implies that a broader range of tree species and sizes than previously thought may contribute functionally important wood to channels. We therefore recommend that survey protocols for streamwood collect information on livewood. Because of livewood's enhanced stability and decay resistance, we also recommend that conceptual models of wood dynamics within channel networks (e.g., Gurnell et al. 2002) and wood-budget models (e.g., Benda and Sias 2003, Gregory et al. 2003b) account for these attributes of livewood. We encourage testing, in diverse forest-stream systems, of the hypotheses we present here (box 1) regarding the geomorphic and ecological roles of livewood.

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